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THE TENDON ORGANS OF CAT MEDIAL GASTROCNEMIUS: SIGNIFICANCE OF MOTOR UNIT TYPE AND SIZE FOR THE ACTIVATION OF Ib AFFERENTS

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SUMMARY

1. Histological and histochemical studies suggest that each tendon organ in a mixed mammalian muscle should be particularly responsive to the contraction of a discrete number of motor units (*ca.* ten to fifteen), each with differing mechanical properties. This report describes physiological experiments that demonstrate this arrangement for the tendon organs of cat medial gastrocnemius.

2. No correlations could be found between the intensity of discharge of a single tendon organ and the contraction strengths of motor units whose contraction excited the receptor. Tendon organs were found to be as responsive to contraction of small slow twitch units as they were to contraction of larger fast twitch units. Taking the data as a whole, the apparent sensitivity of the receptors during motor unit contractions (pps/force recorded at the tendon) was inversely related to the contraction strengths of the motor units.

3. These findings are discussed in relation to recent evidence on the territory of single motor units in medial gastrocnemius and the force producing capabilities of their individual muscle fibres. It is concluded that in general each motor unit, whose contraction excites a given receptor, contributes one muscle fibre to the receptor capsule. Further, it appears that the various excitatory effects of those muscle fibres inserting into a given receptor capsule are not simply related to their relative contraction strengths but also depend on the details of the mechanical coupling between each fibre and the Ib afferent receptor endings.

4. The results of an ensemble analysis show that despite the lack of correlation between the intensity of tendon organ discharge and the force developed at the tendon during contraction of different motor units, a

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correlation does appear when the responses of several tendon organs and the forces developed by the motor units which excite them are summed progressively. This finding has implications for the recruitment order of motor units in that the profile of the collective Ib response is shown to differ according to whether motor unit forces are summed randomly or in order of increasing contraction strengths.

INTRODUCTION

While the structure of Golgi tendon organs is relatively simple (cf. Merrillees, 1962; Bridgman, 1968; Schoultz & Swett, 1972, 1974; Barker, 1974) their mechanical relation with surrounding motor units is complex (Houk & Henneman, 1967; Stuart, Mosher & Gerlach, 1972*a*; Stuart, Mosher, Gerlach & Reinking, 1972*b*). Each tendon organ responds at a very low threshold to the contraction of a small proportion of the parent muscle's motor units; being driven to sustained discharge by some motor units ('in-series' responses) and having stretch discharge decreased by other units ('in-parallel' responses). The present report is concerned with a comparison of excitatory 'in-series' responses to contraction of motor units sharing different mechanical properties.

The structural basis for the study is illustrated in Fig. 1. *A* and *B* are dorsal and lateral views of the medial gastrocnemius from a kitten and show the distribution of tendon organs within the muscle. Each receptor lies 'in-line' with the longitudinal orientation of the surrounding muscle fibres (i.e. from aponeurosis of origin to insertion). Fig. 1*C* shows a typical cross-section of medial gastrocnemius in the adult cat redrawn from a slide provided by V. R. Edgerton (personal communication, see also Edgerton, 1973). Fibres are labelled as *A* (white or fast twitch-glycolytic), *C* (red or fast twitch, oxidative and glycolytic), and *B* (intermediate or slow twitch-oxidative) on the basis of their staining affinity for myosin ATPase and DPNH-diaphorase. Fibres intermediate between *A* and *C* for the DPNH stain are labelled *A-C* (for review of muscle fibre type nomenclature see Close, 1972; Ariano, Armstrong & Edgerton, 1973; Burke & Edgerton, 1975). Ten adjacent fibres are cross-hatched to emphasize how intermingled are different fibre types in this and most other muscles of the cat hind limb. This particular number of muscle fibres is also selected because the capsule of Golgi tendon organs in the cat hind limbs typically clasps the terminations of ten to eleven muscle fibres (Barker, 1974). Contraction of any of these clasped fibres presumably elicits an excitatory effect on the receptor's Ib afferent ending. A variety of indirect but compelling evidence now suggests that motor units are composed of similar fibre types and that motor units occupy overlapping territories (approximately 20 % of the muscle's cross-section) with the majority of each unit's fibres not directly adjacent to each other (Edström & Kugelberg, 1968; Kugelberg & Edström, 1968; Burke, Levine, Zajac, Tsairis & Engel, 1971; Brandstater & Lambert, 1973; Burke, Levine, Tsairis & Zajac, 1973; Burke & Tsairis, 1973). With such evidence in mind it can be proposed that the ten-fibred matrix of Fig. 1*C* could receive contributions from ten

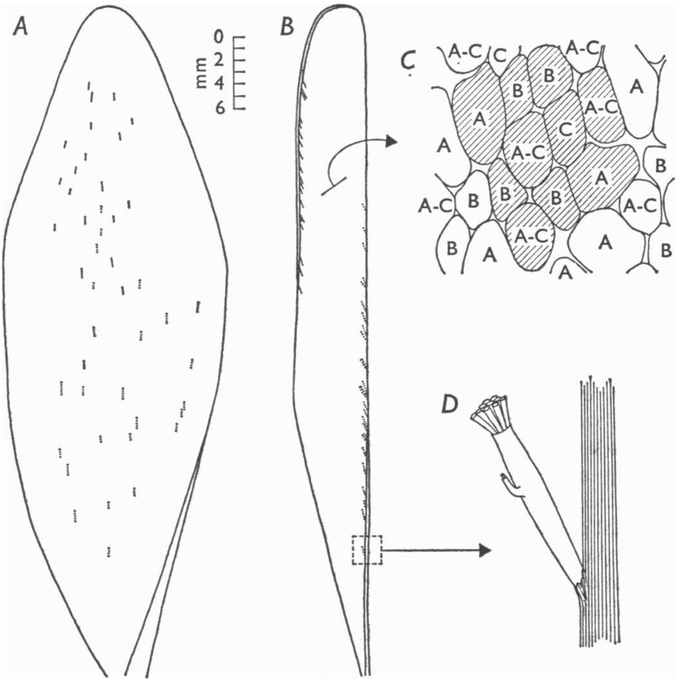

Fig. 1. A schematic view of the relationship between muscle fibres and tendon organs in cat medial gastrocnemius. *A* and *B* are modified from Swett & Eldred (1960) and show a dorsal (*A*) and lateral or imaginary sagittal (*B*) view of the left medial gastrocnemius muscle in a 1 kg kitten. Tendon organs beneath the superficial aponeurosis of origin are shown with continuous lines and those lining the deep distal aponeurosis with interrupted lines. There are forty-four tendon organs in all: twenty-five proximal and nineteen distal. Not included are receptors within the tendon proper which usually comprise about 7 % of the total number (Barker, 1974). *C* shows a typical cross-section of adult cat medial gastrocnemius. Fibres are labelled *A*, *B*, *C* and *A-C* on the basis of their histochemical type (see text for details). *D* is modified from Schoultz & Swett (1972) and shows the manner in which the capsule of a single tendon organ is connected to the aponeurosis of insertion (or origin) at one end and clasps ten to eleven fibres at the other end. A scale is not provided for *D*. The total length of the tendon organ capsule ranges from 500 to 1200 μm and the diameter at mid-section from 100 to 120 μm (for review see Stuart *et al.* 1972*a*).

different motor units. Further, there is now good evidence to suggest that slowly contracting motor units in medial gastrocnemius are largely composed of B fibres, and fast twitch highly fatigable, non-fatigable and intermediately fatigable units of *A*, *C* and *A-C* fibres respectively (Burke *et al.* 1973; Burke & Edgerton, 1975). Thus we may propose that each tendon organ in cat medial gastrocnemius should respond to the contraction of a discrete number of motor units sharing a range of contraction times and fatigue resistance. This report describes physiological experiments that demonstrate this arrangement. A preliminary account has been presented (Stephens & Stuart, 1974).

METHODS

Experiments were performed on nine adult cats anaesthetized with pentobarbitone sodium.

Recording

The discharges of single Ib afferent fibres from the left medial gastrocnemius muscle were recorded from dorsal root filaments. All nerves to the hip, tail and hind limb were cut, leaving the nerve to medial gastrocnemius intact. Dorsal and ventral roots L6 to S2 were cut on the left side.

Ib afferents were functionally isolated from subdivided dorsal rootlets and identified on the basis of their group I range conduction velocity and their accelerated response during an isometric twitch of the whole muscle (cf. Matthews, 1972). Spindle afferents sometimes also fire repetitively during the rising phase of twitch tension in medial gastrocnemius. If doubt persisted the whole muscle was stimulated at 10–25 pulses/sec and stimulus strength adjusted to fire the majority of α fibres and a minimum of γ fibres (i.e. an 80–90 % contraction). This procedure resulted in sustained Ib firing while gamma activated spindle discharge is either absent or intermittent. The procedure could still produce a β-activated spindle discharge (cf. Barker, 1974) but β motor fibres to medial gastrocnemius are presumably rare and of relatively high (γ range) electrical threshold. Ib afferent conduction velocity was measured by stimulating the muscle nerve and recording the conducted impulse at the dorsal root filament. Conduction distance was estimated at the end of the experiment by lying a piece of silk thread along the course of the nerve dissected free in its entirety except for that portion lying within the intervertebral foramen. The length of this portion was estimated by laying the thread over the bones (cf. Matthews, 1963). The afferent conduction velocities ranged from 79 to 130 m/sec with an average (± S.D.) of 101 ± 13 m/sec.

The left medial gastrocnemius muscle was carefully freed from its surrounding attachments without compromising the blood supply. The animal was held to a rigid Göteborg-type metal frame with clamps, the left knee being flexed at an angle of 130°. Clamps were fixed to the proximal and distal ends of the tibia and to the condyles of the femur. Motor unit isometric tension and whole muscle passive tension were measured using a strain ring mounted on a rotary table (Reinking & Stuart, 1974). The total compliance of the muscle tendon, its attachment to the strain ring and the ring itself was $< 300\ \mu$/kg (Reinking, Stephens & Stuart, 1975). In order to measure the small forces developed during motor unit contractions in the presence of relatively large passive tensions a 'track and hold' back off circuit

(Reinking & Stephens, 1975) similar to that described by Buller & Lewis (1965) was used. The over-all noise of the system for measuring motor unit forces was 150 mg r.m.s.

Mineral-oil pools covered the lumbar cord and medial gastrocnemius. The temperature at the rectum and muscle oil pool were independently maintained at 37 ± 1° C by thermistor controlled heaters.

Isolation of single motor units

Motor units were isolated for study by dissection of ventral root filaments using the technique described by McPhedran, Wuerker & Henneman (1965). This technique always raises the possibility that functionally isolated 'single' α axons are in fact two axons with almost identical thresholds (Norris & Irwin, 1961), particularly if one of the units develops much more force than the other. As an added precaution we therefore routinely measured the e.m.g. response with stimulus set at threshold. If two axons are present then the e.m.g. signal shows activation of sometimes one or the other or both (see also Bagust, Knott, Lewis, Luck & Westerman, 1973).

Motor units were selected whose contraction elicited sustained discharge of the tendon organ under study. It has been reported that a tendon organ will only respond to contraction of a motor unit if that motor unit contributes at least one muscle fibre to the capsule of the receptor (Houk & Henneman, 1967). In our laboratory we have often noted, however, that a Ib afferent may respond quite vigorously to co-contraction of two units but not to contraction of one or the other unit alone. While there is an obvious need for glycogen depletion and subsequent reconstruction of the mechanical relations involved in this and similarly complex findings (cf. Stuart *et al.* 1972*b*), the problem will never be easily disposable for those experiments in which more than one Ib afferent and more than one or two motor units have to be studied. For the present analysis we rejected those instances in which Ib discharges in response to contraction of a single motor unit failed either (1) to increase by $\geqq$ 5 pulses/sec over at least a 6 mm range of muscle length during establishment of the motor unit's length-tension curve; or (2) to increase by $\geqq$ 10 pulses/sec over a 4 mm range of muscle length. These arbitrary criteria are a compromise between not wishing to report 'off-line' responses (Stuart *et al.* 1972*b*) and yet not rejecting the possibility that some tendon organs might indeed have relatively high thresholds or relatively sluggish firing to 'in-series' contractile force.

Characterization of motor unit type

In the present report the mechanical properties of a motor unit are characterized by its peak tetanic tension, twitch contraction time and fatigability.

Peak tetanic tension was measured at the optimum length for tetanus of each unit. Fast twitch units (contraction time $\leqslant$ 45 msec) were stimulated at 200 pulses/sec for either 500 or 800 msec, the longer duration stimulus used only for the more fatigue resistant units. Slow twitch units (contraction time $>$ 45 msec) were stimulated at 100 pulses/sec for 1·5 sec. Twitch contraction time was measured from the onset of the e.m.g. to the peak force developed at the optimum length for twitch of each unit after potentiation. For fast twitch units, twitch potentiation was produced by stimulating at 200 pulses/sec for 600 msec 2 sec before each twitch. This procedure was repeated every 10 sec until the twitch amplitude reached a maximum. For slow twitch units the pre-twitch tetanus involved 100 pulses/sec stimulation for 1·5 sec.

Fatigability was estimated from the cumulative force profile resulting from 4 min stimulation at 40 pulses/sec for 330 msec of each second. The fatigue index used in this study denotes that percentage of cumulative force developed after 2 min of the

4 min stimulation period. Non-fatigable units have an index close to 50% and highly fatigable units near 100% (for details see Stephens, Gerlach, Reinking & Stuart, 1973).

Setting of muscle length

As described elsewhere (Stephens, Reinking & Stuart, 1975*b*), the apparent static sensitivity of a Golgi tendon organ depends on muscle length. Thus in the present study a standard length setting was chosen for each receptor. This length was not the same for each receptor but corresponded to a length which was close to the optimum length for each of the individual motor units found to excite the receptor and where possible at a length where there was no spontaneous Ib afferent discharge (i.e. no 'passive' firing to the passive tension). In those cases where the Ib afferent exhibited passive firing at very short muscle lengths (five of twenty-three receptors), the Ib afferent response (Δr) to the active motor unit contractions was estimated by subtracting the spontaneous firing rate from the total firing rate achieved during the active contractions (for description of changes in spontaneous Ib afferent discharge with muscle length see Stephens *et al.* 1975*b*).

Analysis

Data was analysed during the experiments using a small laboratory computer (Digital Equip. Corp. Lab 8/e).

Before each motor unit tetanic contraction, the passive Ib firing rate (if any) was measured by counting the number of spikes in a 1 sec period. During each contraction, the average Ib firing rate and average active force developed was estimated. For fast twitch units (CT $\leqslant$ 45 msec) force was measured by averaging successive force samples taken at 10 msec intervals starting 200 msec after the onset of the contraction (stimulus rate 200 pulses/sec) and continuing to 500 msec for the more fatigable fast twitch units (stimulus duration 500 msec) and to 700 msec for the fatigue resistant fast twitch units (stimulus duration 800 msec). For slow twitch units (contraction time > 45 msec) force samples were taken at 20 msec intervals starting 400 msec after the start of stimulation (stimulation rate 100 pulses/sec) and continuing to 1400 msec (stimulus duration 1·5 sec). The average Ib firing rates were estimated by counting the number of afferent spikes recorded during the respective averaging periods. In this way only the static Ib responses were studied (for dynamic Ib responses see Stephens *et al.* 1975*b*).

RESULTS

The responses of 23 Ib afferents to contraction of fifty-seven different motor units have been studied in nine experiments. Each interaction between a tendon organ and a motor unit was studied for 30–60 min. One afferent was activated by five motor units, five by four motor units, four by three motor units, seven by two motor units and six afferents by one motor unit. Responses of eight other afferents to contraction of eleven additional motor units are not included because the responses were considered too feeble (see Methods) to indicate a tight coupling between the receptor and the exciting force.

Fig. 2 shows tridimensional histograms of the size, contractile speed and fatigability of four different groups of motor units whose contraction elicited sustained discharge in four different Ib afferents. Note that in all cases the motor units exhibited a broad range of mechanical properties. This point is further emphasized in Table 1 which lists the range of mechanical properties for groups of 3, 4 and 5 motor units whose contraction elicited sustained discharge in ten different Ib afferents (see also Table 3). Not shown in Table 1 are seven other afferents which responded to contraction of two motor units each. Even within these small samples the range of mechanical properties was quite obvious. Taken together the data support the view that each tendon organ is capable of responding to

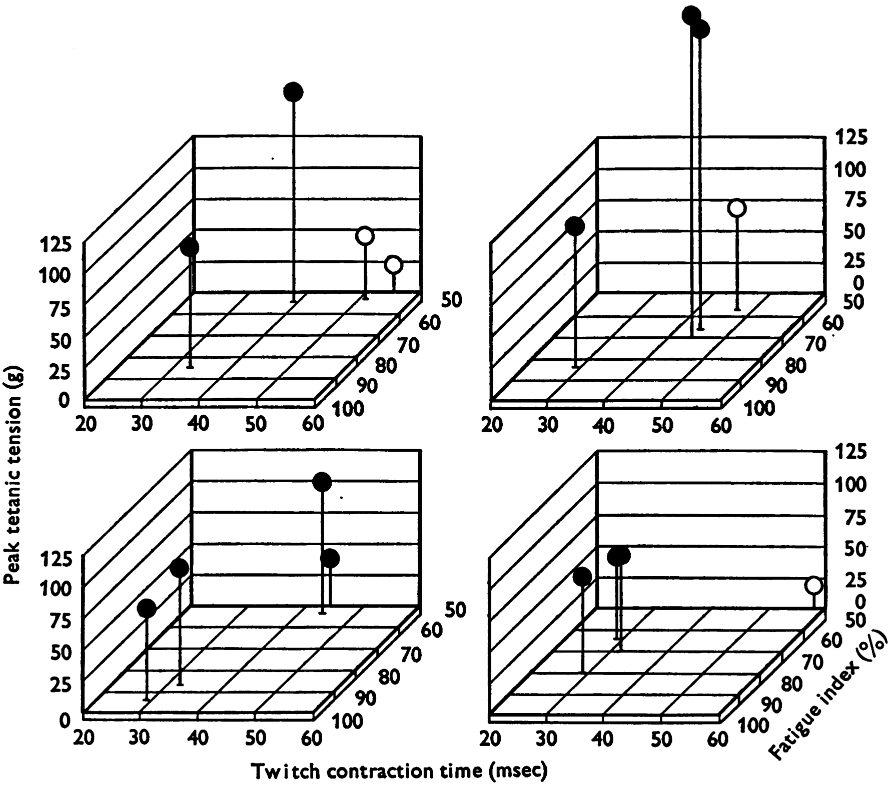

Fig. 2. Tridimensional histograms illustrating the range in mechanical properties for medial gastrocnemius motor units whose contraction elicited sustained discharge in the same Ib afferent from a tendon organ. Fast twitch units (contraction time $\leqslant$ 45 msec) have filled circle tops and slow twitch units ($>$ 45 msec) have open circle tops. *Y* axes indicate peak tetanic tension at optimal muscle length for each motor unit, *X* axes the contraction time of the fully potentiated twitch and *Z* axes the fatigue index. Non-fatigable units have a fatigue index near 50% and highly fatigable units are near 100%. Note that all four Ib afferents are activated by motor units with a broad range of mechanical properties.

contraction of motor units with a broad range of mechanical properties. These findings invite comparison of the firing rates attained by a single tendon organ during contraction of its several exciting motor units.

TABLE 1. Range in properties for motor units whose contraction elicited a sustained discharge in a single tendon organ

Sample			Motor unit characteristics		
Expt. no.	Tendon organ no.	No. of motor units	Peak tetanic tension* (g)	Twitch contraction time† (msec)	Fatigue index‡ (%)
10	1	4	22—166	33—55	50—85
11	1	4	80—254	29—47	57—84
12	2	3	15—154	32—68	53—67
	3	3	66—116	33—44	57—72
13	1	4	38—104	29—44	50—94
	2	3	23— 89	32—66	50—81
17	3	4	18— 75	29—58	50—80
20	1	3	6— 45	26—66	73—79
23	4	4	18—101	28—40	49—86
	7	5	36— 87	25—33	52—84

* Measured at optimal position on each motor unit length–tension curve.

† Measured at optimal position on each motor unit length–tension curve after potentiation.

‡ Percentage cumulative force developed at 2 min in a 4 min fatigue test. For details see Stephens *et al.* (1973).

TABLE 2. Lack of relation between the changes in firing rate of Ib afferents and the force recorded at the tendon during contraction of single motor units*

Afferent 1			Afferent 2			Afferent 3		
Δf† (g)	Δr‡ (pulses/sec)	$\Delta r/\Delta f$ (pulses/sec.g)	Δf (g)	Δr (pulses/sec)	$\Delta r/\Delta f$ (pulses/sec.g)	Δf (g)	Δr (pulses/sec)	$\Delta r/\Delta f$ (pulses/sec.g)
18	78	4·33	45	33	0·73	16	55	3·44
48	70	1·46	103	18	0·17	17	27	1·59
71	71	1·00	198	108	0·55	71	98	1·38
149	45	0·30	209	15	0·07	75	40	0·53

* Note that each afferent's firing rate is shown in relation to contraction of a different set of motor units.

† Tetanic tension of a motor unit minus whole muscle passive tension (if present). See text for details on the setting of muscle length.

‡ Increase in Ib afferent firing rate during motor unit contraction.

Apparent and absolute sensitivity of tendon organs to active force developed by single motor units

The present data show that there is no correlation between the Ib firing rate attained and the forces developed at the tendon when the responses of a single afferent to the contraction of several motor units are compared. In Table 2 for example, Δr values for three different Ib afferents are shown in relation to the Δf values for groups of 4 of their exciting motor units. The Δf values are ranked according to their size. This ranking does not lead to similar ranking of Δr values, however. Such ranking was explored for one afferent activated by five motor units, five afferents activated by four units, and four afferents activated by three units. In only one set of Ib–motor unit interactions was there a similar ranking for Δf (three units) and Δr. Similarly for the seven afferents studied with but two motor units each, the data showed no predictable relationship between Δr and Δf.

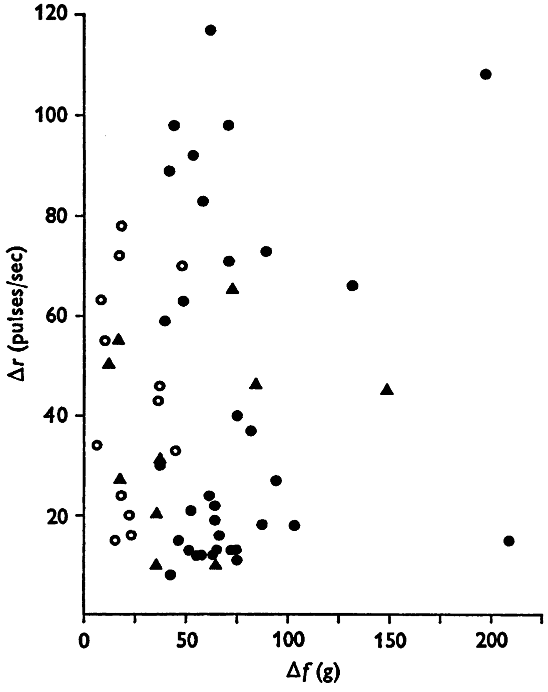

Fig. 3. The lack of relationship between Ib afferent firing rate (Δr in pulses/sec) and active contractile force (Δf in g) developed by their excitatory motor units. Slow contracting motor units are shown by open circles, fast non-fatigable units with filled triangles and fast fatigable units with filled circles. See Methods for description of muscle length settings for data in this and Figs. 4–6.

This point is further emphasized for the total data in Fig. 3, which shows the Δr values of twenty-three Ib afferents and the corresponding Δf values for fifty-seven motor units. The coefficient of linear correlation between Δr and Δf was insignificant ($P > 0{\cdot}1$). In this and subsequent Figures, data obtained during contraction of slow twitch units (contraction time > 45 msec), fast twitch (contraction time $\leqslant$ 45 msec) non-fatigable units and fast twitch fatigable units are shown separately (see Figure legend).

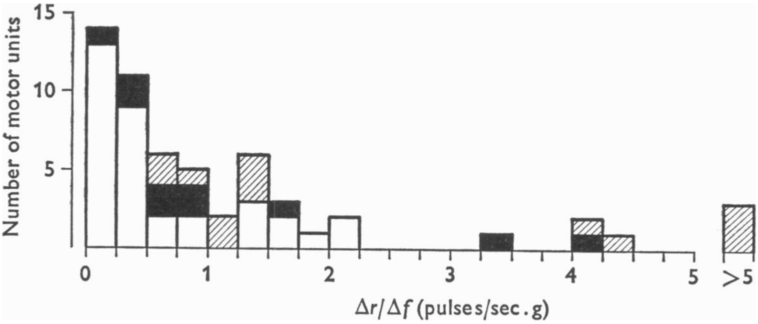

Fig. 4. The distribution of 'apparent sensitivity' ($\Delta r/\Delta f$) for twenty-three Ib afferents activated by fifty-seven motor units. Slow twitch units are shown cross-hatched while dark hatching is for fatigue resistant fast twitch units (fatigue index $\leqq 55\%$).

The apparent sensitivity of a tendon organ to contraction of a single motor unit is conveniently expressed as the ratio of its response (Δr) to the active force developed by the unit (Δf) as measured at the tendon of insertion. Fig. 4 shows the distribution of apparent sensitivities for the fifty-seven Ib-motor unit interactions of this study. Notice that fast twitch-fatigable units had $\Delta r/\Delta f$ values generally $< 0{\cdot}5$ pulses/sec.g while the other two categories had values generally $> 0{\cdot}5$ pulses/sec.g. Apparent sensitivities $> 3{\cdot}0$ pulses/sec.g were only encountered among slow twitch and fast non-fatigable units. This point is further emphasized in Fig. 5 with apparent sensitivity plotted against Δf for each of the fifty-seven Ib–motor unit interactions. As the size of a motor unit decreases there is a progressive increase in the apparent sensitivity of the tendon organ response. Assuming a power law relationship, the best fit equation was $\Delta r/\Delta f = 39{\cdot}8\Delta f^{-1{\cdot}07}$.

The lack of relation between Δr and Δf and the existence of a relationship between $\Delta r/\Delta f$ and Δf is in keeping with the mechanical arrangement shown in Fig. 1. Tendon organs typically clasp ten to eleven muscle fibres, each of which must usually come from a different motor unit (see Discussion). The most significant active force input to a tendon organ comes from contraction of those single fibres directly in series with it rather than from the total force developed by the units to which the fibres belong. Viewed in this light Fig. 5 simply reflects the fact that the smaller the Δf, the greater the proportion of this force is applied directly to the receptor.

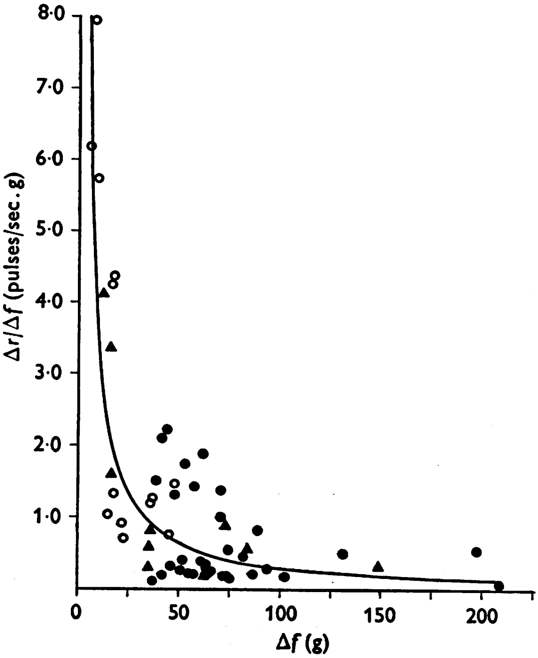

Fig. 5. Relationship between the 'apparent sensitivity' ($\Delta r/\Delta f$) for twenty-three Ib afferents activated by fifty-seven motor units and the active contractile force (Δf) of the motor units. Slow twitch motor units indicated with open circles and non-fatigable fast twitch units with filled triangles. A power curve line of best fit is shown ($Y = 39{\cdot}8X^{-1{\cdot}07}$; $r = -0{\cdot}7$, $P < 0{\cdot}001$) to emphasize the progressive increase in 'apparent sensitivity' of a tendon organ's responses when the exciting motor units become progressively smaller.

Sensitivity to contraction of different types of motor units

The absolute sensitivity of a tendon organ to active contractile force can be expressed as the ratio of its response (Δr) to the force exerted *directly* on the receptor capsule. In experiments of the present kind this force cannot be measured in absolute terms, although it can be computed indirectly in arbitrary units (Stephens *et al.* 1975*b*). For the present purposes, it is sufficient to point out that the Ib firing rate alone gives some indication of the force exerted on the receptor, high firing rates being presumably associated with high forces and vice versa.

Fig. 6 shows the distribution of Ib firing rates for the twenty-three afferents when activated by contraction of fifty-seven motor units. These rates ranged from 8 to 117 pps with a mean of 41 pulses/sec (± S.D. 30 pulses/sec). It is a unimodal but asymmetrical distribution with twenty-six of the fifty-seven responses between ten and thirty p.p.s. The three categories of motor units are compared again, to reveal a particularly thought-provoking point. Taking the data as a whole it is clear that Ib afferents can respond as vigorously during contraction of small, slow contracting units as they can during contraction of any other type of unit. For this particular sample the mean firing rates attained during contractions of slow contracting, fast contracting non-fatigable and fast contracting fatigable units were not significantly different (mean firing rates 44, 36 and 42 pulses/sec respectively, 2-tail *t* tests $P > 0{\cdot}1$).

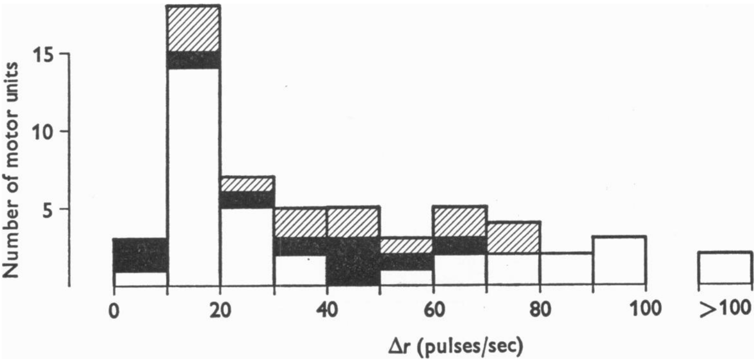

Fig. 6. The distribution of firing rates (Δr) for twenty-three Ib afferents activated by contraction of fifty-seven motor units. Cross-hatching marks slow twitch motor units while dark hatching is for fast twitch motor units of low fatigability (fatigue index ≦ 55 %).

This finding is of particular interest in relation to the recent estimates by Burke & Tsairis (1973) of the intrinsic force producing capabilities of fast and slow twitch muscle fibres in cat medial gastrocnemius. It may be calculated from these estimates that individual slow twitch fibres generate not more than one-eighth of the force of fast twitch fibres (see also Discussion). Thus for any given tendon organ, contraction of slow twitch units would have been expected to exert a far smaller excitatory effect than contraction of fast twitch units. In the present data, however, where comparison could be made between the response of a given tendon organ to contraction of an unequivocal type S unit (contraction times ⩾ 55 msec, no 'sag' in an unfused tetanus; cf. Burke *et al.* 1973; Burke & Tsairis, 1973) and its response to contraction of fast twitch units, in only two tendon organs did contraction of the slow twitch units elicit the weakest response (see Table 3, afferents 1 and 2). In the remaining cases the firing rate recorded during contraction of the slow twitch units was either the same (afferent 3, Table 3), intermediate (afferent 4, Table 3) or greater (afferent 5, Table 3) than that recorded during contraction of the fast twitch units. While it is true that firing rates > 80 pulses/sec were only encountered during contraction of fast contracting fatigable units, it is nevertheless clear that if changes in Ib firing rate (Δr) are indicative of changes in force exerted at the receptor capsule, then these changes must be relatively similar during contractions of motor units of different mechanical type, despite the apparent differences in the contraction strength of their individual muscle fibres.

TABLE 3. Mechanical properties of motor units and their excitatory effects on single Ib afferents

Afferent no.	Motor unit no.	Contraction time* (msec)	Fatigue index† (%)	Δf‡ (g)	Δr§ (pulses/sec)	$\Delta r/\Delta f$ (pulses/sec.g)
1	1	66	73	6	34	5·67
	2	26	76	39	59	1·51
	3	27	79	42	89	2·12
2	1	66	53	22	20	0·91
	2	53	50	18	24	1·33
	3	32	81	82	37	0·45
3	1	68	53	15	15	1·00
	2	32	62	46	15	0·33
	3	41	67	132	66	0·50
4	1	29	64	48	63	1·31
	2	58	50	17	72	4·24
	3	29	80	58	83	1·43
	4	31	69	62	117	1·89
5	1	39	54	149	45	0·30
	2	51	53	48	70	1·46
	3	33	85	71	71	1·00
	4	55	50	18	78	4·33

* Measured at optimum length for twitch after potentiation.

† Percentage cumulative force developed at 2 min in a 4 min fatigue test.

‡ Active force developed.

§ Change in Ib firing rate during active force developed.

Ensemble Ib response

While the firing rate attained by a single Ib afferent is not related to the forces generated at the tendon by different motor units acting on the receptor, we can hypothesize that the ensemble or collective response of several tendon organs might nevertheless be expected to be related to the total active force generated by the muscle.

In order to test this hypothesis, the responses of twelve Ib afferents to contractions of twenty-seven motor units have been summed. The data are from five experiments with muscle length set in each case at −4 mm relative to the parent whole muscle tetanic tension optimum length. In Fig. 7*A* the twenty-seven motor units were first ranked according to their tetanic tensions. These tetanic tensions were then summed cumulatively and plotted against the fraction of the sample used to form each sum.

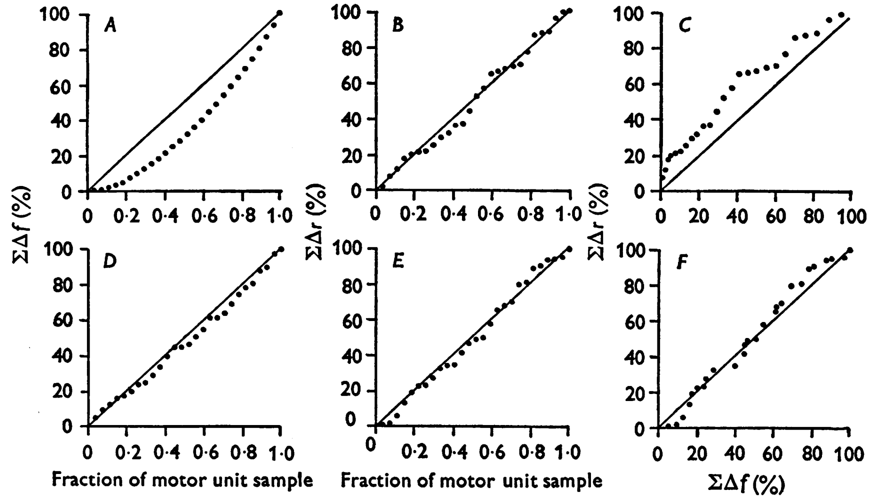

Fig. 7. The 'ensemble' Ib response and its relationship to cumulative force development by motor units. In *A* and *D* the Δf values for individual motor units are summed in cumulative fashion along the *Y* axis and the fraction of motor units used in the summation shown on the *X* axis. *B* and *E* plots have the same *X* axis with Δr values now summed in cumulative fashion along the *Y* axis. *C* and *G* have the same *Y* axis as *B* and *E* with Δf now summed cumulatively along the *X* axis. For *A*, *B* and *C* motor units are summed in order of increasing contraction strength while in *D*, *E* and *F* the motor units are summed in random fashion. In each plot a line has been drawn to indicate a proportional relationship between the *X* and *Y* variables.

The resulting curve is convex to the *X* axis because the distribution of tetanic tension in this motor unit sample was essentially rectangular. The 45° line would be expected if all the units developed the same tetanic tension. In Fig. 7*B* the corresponding Ib firing rates attained during contraction of these motor units have also been summed progressively. This cumulative curve lies very close to the 45° line as would be expected if there were no relationship between tetanic tension developed and the Ib firing rate attained. In Fig. 7*C* the curves of Fig. 7*A* and *B* have been combined and the cumulative force shown on the *X* axis and the cumulative Ib firing rate on the *Y* axis. The 45° line would be expected if the cumulative firing rates attained were proportional to the cumulative force. Notice that the curve in 7*C* is concave to the *X* axis, indicating that at low cumulative force levels the ensemble Ib input is relatively more powerful than at high force levels, which simply reflects the fact that in general small motor units can excite Ib afferents as strongly as larger motor units.

In Fig. 7*D*, *E* and *F* essentially the same procedures are used as in Fig. 7*A*, *B* and *C* except that the motor units have in this case been ranked in random order. Notice that this procedure results in a cumulative curve in Fig. 7*D* which is close to the 45° line. Such a result reflects the fact that the motor unit sample contained an essentially rectangular distribution of tetanic tensions. In Fig. 7*E* the corresponding cumulative Ib response is again close to the 45° line. In this case such a result would be expected if the relationship between the Ib firing rate achieved were either proportional or randomly related to the corresponding forces developed by the motor units. In Fig. 7*F* cumulative curves of Fig. 7*D* and *E* are combined. Notice that in contrast to Fig. 7*C* the curve relating cumulative force and Ib response lies close to the 45° line.

Although there are some restrictions on the functional significance of this analysis due to current uncertainties on the usage rate and recruitment order of motor units (cf. Grillner, 1972; Goslow, Reinking & Stuart, 1973; Stephens & Stuart, 1975), these results do indicate that despite the lack of correlation between Ib firing and the forces developed by its exciting motor units at the tendon, the ensemble response of several Ib afferents is related to the total force developed by the muscle.

DISCUSSION

The present results show that a single tendon organ is responsive to contraction of motor units of widely different mechanical properties. This finding supports a variety of histological and histochemical studies (cf. Burke & Tsairis, 1973), which indirectly suggest that the muscle fibres inserting into the receptor capsule are not selected in any way but contain a mixture of fibre types in keeping with the overall composition of the muscle. These data also demonstrate that the responses of tendon organs to different types of motor unit are in many cases relatively similar. Before discussing the significance of this observation it is necessary to consider how many muscle fibres from a single motor unit might be inserted into a given receptor capsule.

Motor unit contributions to the capsule of a tendon organ

As yet there is no direct experimental evidence on the number of muscle fibres contributed by a single motor unit to a given receptor capsule, but some estimates can be made on the basis of a detailed account of the anatomy of medial gastrocnemius motor units recently provided by Burke & Tsairis (1973). These authors found that the muscle fibres of a single motor unit were diffusely and relatively evenly distributed amongst fibres belonging to other motor units, with very few adjacent muscle fibres belonging to the same unit. Similarly Brandstater & Lambert (1973) found on the average that 76 % of the fibres in rat anterior tibial units were separate from each other and that there was no greater tendency for grouping of fibres in motor units than in random model units. If these data are considered in relation to the number of muscle fibres inserted into each tendon organ capsule, it is possible to estimate the number of motor units contributing muscle fibres to each receptor. According to Bridgman (1968) tendon organs are attached to between eight and twenty-five muscle fibres. Barker (1974) reports a similar range of three to twenty-five muscle fibres (mean 10·5) with only 5 % of the sample examined attached to more than twenty-five muscle fibres.

Assuming a maximum density of motor unit muscle fibres of 5 per 100 total fibres (Burke & Tsairis, 1973) we may calculate that considering a population of forty muscle fibres the probability of a single motor unit contributing a single fibre to a matrix of ten to eleven adjacent fibres is 0·4. The probability of a single unit contributing two muscle fibres is very much less (0·06). This difference in probability becomes progressively smaller as the matrix size is increased. For example, the probabilities of finding one muscle fibre from a single motor unit in matrices of twenty and twenty-five muscle fibres are 0·51 and 0·48 respectively, whereas the corresponding two fibre probabilities are 0·24 and 0·38.

The probability calculations were made by first choosing a parent population of forty muscle fibres. A population of this size was used for convenience, and calculations based on larger sized populations do not alter the general result. Calculation of the probabilities was then based on a figure of 0·05 for the probability of a single muscle fibre from a single motor unit occurring in the parent population (Burke & Tsairis, 1973). For a given matrix size the calculation of the probability of finding one or two single motor unit fibres was made by considering the probability of finding such a fibre (or fibres) each time successive fibres were removed from the parent population until the matrix was complete. Such a procedure takes into account the fact that completion of the matrix resulted in a progressive change in the composition of the parent population and hence the probability of removing a motor unit fibre. The simpler binomial distribution, while giving essentially the same results was not used because under the present circumstances the assumption of a stationary parent population seemed inappropriate.

Although the probability of finding one muscle fibre from a single motor unit in a given matrix first rises as the matrix size increases, it does subsequently reach a maximum and then falls because after a critical size is reached the probability of finding two muscle fibres begins to outweigh the possibility of finding a single fibre. It is perhaps significant that this critical point is reached with a matrix size of about 20, close to the upper limit for the number of muscle fibres inserted into the majority of tendon organ capsules.

On the basis of these calculations it seems clear that the ten to eleven muscle fibres inserting into the *average* tendon organ are usually contributed by ten to eleven separate motor units. It is not implied, of course, that tendon organs cannot be found with more than one fibre contributed to their capsules by a single motor unit. Rather it is envisaged that, like the grouping of motor unit fibres, such occurrences are both rare and random and not in line with the main design features of the muscle.

If we can assume, therefore, that in general each motor unit supplies only one muscle fibre in series with a given receptor, then the observation that motor units of different mechanical type can exert a similar excitatory effect on a given tendon organ suggests that the increased force exerted on the receptor capsule during contraction of the corresponding different types of muscle fibre was generally similar. Such a conclusion invites discussion of the available estimates of the contraction strength of muscle fibres belonging to motor units of different mechanical type.

Force generating capabilities of single muscle fibres

Recently, Burke & Tsairis (1973) have made some indirect estimates of the innervation ratios of their FF, FR and S type units in medial gastrocnemius. On the basis of this data and the tetanic tensions they reported for the different unit types, it may be calculated that the average force developed by single muscle fibres of the fast twitch highly fatigable, fast twitch fatigue-resistant and slow twitch units in their study was 0·089, 0·085 and 0·011 g respectively (force per muscle fibre = tetanic tension/average number of muscle fibres). These data indicate a striking difference between the contraction strengths of fast and slow twitch muscle fibres but similar values for highly fatigable and fatigue-resistant fast twitch fibres.

While these findings are consistent with the fact that in the present study fatigue-resistant and highly fatigable motor units exerted similar excitatory effects on a given tendon organ, the excitatory effects of slow twitch units were also generally similar and not, as would have been expected, considerably smaller. Certainly the responses to contraction of slow twitch units were never 8 or 9 times weaker as might have been predicted. This somewhat unexpected result led us to seek for some explanation based on the recent detailed anatomical description of this receptor by Schoultz & Swett (1972, 1974).

Mechanical arrangement between a tendon organ and its associated muscle fibres

The following description is a resumé of the findings of Schoultz & Swett (1972, 1974) and the reader should consult the original papers for a more detailed account.

Each Golgi tendon organ encloses at its proximal end the collagenous terminations of a number of muscle fibres. Immediately distal to the proximal capsule collar, septal cell compartments are formed around the collagenous bundles of one to three muscle fibres. These compartments soon merge with others, however, such that for the greater part of the length of the tendon organ the receptor capsule is divided into irregularly shaped longitudinally running compartments containing a mixed collection of collagen fibres from a number of different muscle fibres. The Ib afferent enters the receptor capsule in its equatorial region and enters a central compartment largely devoid of collagen. Within this compartment the axon divides into myelinated branches which run longitudinally, proximally and distally. Periodically these branches give rise to unmyelinated collaterals which pass radially to enter the more peripherally located compartments containing loosely arranged bundles of collagen. Once within such a compartment these preterminal axons branch extensively to form spirals around discrete collagen bundles which are twisted and intertwined around one another rather like the strands of a braided rope.

With this anatomical arrangement in mind, Schoultz & Swett (1972) proposed that increases in force in series with the receptor cause the collagen bundles to straighten, thereby twisting and pinching large surface areas of the terminal Ib axonal branches trapped between them. Such distortion presumably then finally leads to the repetitive firing of the parent Ib afferent.

In the present context the most important feature of this anatomical arrangement is that it implies that the force developed during contraction of a single muscle fibre is distributed along the complicated ramifications of its own original collagen termination and those of other muscle fibres finally to distort the unmyelinated Ib afferent endings in several different septal compartments. In view of this complicated mechanical coupling it seems clear that the details of this arrangement might play an important part in determining the force-firing rate characteristics of an individual muscle fibre–receptor interaction. Indeed such differences in the net mechanical advantage between muscle fibres and the receptor endings might explain our finding that an apparently much weaker slow twitch fibre can, on occasion, exert a greater excitatory effect on a given receptor than a fast-twitch fibre.

Alternatively on these same anatomical grounds, it could be argued that contraction of a single muscle fibre might only be capable of producing limited distortion of the Ib afferent terminals (cf. Schoultz & Swett, 1972). The existence of such a saturation effect at the single motor unit level is supported by our recording of Ib afferent activity during fatiguing motor unit contractions (Stephens *et al.* 1975*b*). In this situation tendon organ discharge has been observed to remain constant despite reductions in motor unit contraction strength until a point is reached where the receptor discharge begins to decrease in parallel with the continued fatigue of the motor unit. Once again the level of force exerted at the receptor capsule at which this saturation occurs presumably depends on the detailed mechanical coupling between the force exerted by the muscle fibre and the receptor endings. A mechanism of this sort could explain why such relatively limited differences in firing rate were often observed during contraction of fast and slow motor units on the same receptor (see Table 3). Such a saturation effect at the single muscle fibre level does not, of course, imply that further increases in Ib afferent firing cannot take place as additional muscle fibres become active.

The collective behaviour of tendon organs and its possible significance during normal muscle contractions

Despite the lack of relationship between force developed at the tendon and the discharge rate of tendon organs at a single motor unit/tendon organ level, the collective response of a number of tendon organs is related to the total force summed at the tendon (Fig. 7).

One important limitation to this analysis is the possibility that during normal muscle contractions there might be a significant number of motor units whose contraction does not affect the discharge of any tendon organ and thus would be able to increase the force developed by the muscle without increasing the overall tendon organ discharge. This situation is, however, unlikely in view of the relative numbers of motor units and tendon organs within medial gastrocnemius.

If we assume that there are forty-four tendon organs in gastrocnemius (Swett & Eldred, 1960), each connected to an average of 10·5 muscle fibres (Barker, 1974), then we may calculate that the maximum possible number of motor units that could be connected to these tendon organs is 462 (10·5 × 44). This number is greater than the 280 motor units reported by Boyd & Davey (1968) for medial gastrocnemius. Clearly this result can be explained either on the basis that each motor unit contributes more than one muscle fibre to a given tendon organ or that some motor units are connected to more than one receptor. As described previously, however, although the first possibility probably occurs, it is unlikely unless the number of muscle fibres attached to a tendon organ is large (i.e. > 20). On the other hand, if we suppose that a motor unit can contribute a single muscle fibre to one tendon organ or a single muscle fibre to each of two tendon organs, we can calculate that of the 280 motor units, ninety-eight would contribute a single muscle fibre to a single tendon organ and 182 would contribute a single muscle fibre to each of two tendon organs. Such an arrangement points to a very close and powerful association between motor units and tendon organs. Certainly the spacing of tendon organs along the borders of the muscle (Swett & Eldred, 1960) is sufficiently close and the territory of a given motor unit sufficiently large (approximately 4 cm, Burke & Tsairis, 1973) to allow this arrangement.

The present ensemble analysis is considered to have been particularly valuable because it revealed that the relationship between the collective tendon organ discharge and force developed at the tendon depends on the order in which the motor unit/tendon organ responses are summed. When the units are added in order of increasing tension, there is at first a relatively large increase in total tendon organ response which then tends to increase less rapidly as further units are added. If this situation is representative of normal tendon organ/motor unit behaviour, then it suggests that during relatively weak contractions the collective tendon organ discharge from the muscle is relatively stronger than during larger contractions. On the other hand, if the units are added in random order a near linear relationship between total tendon organ discharge and force would be expected.

It is clear that any extension of this ensemble analysis should involve simultaneous recording of several Ib afferents during normal muscle contractions. A simple approach to this problem would be to record the activity of Ib afferents and changes in muscle force during reflex or brainstem stimulation in the anaesthetized or decerebrate cat (cf. Houk, Singer & Goldman, 1970). The results of such experiments could test our current hypothesis that information concerning changes in total muscle force is contained in the collective discharge of many tendon organs rather than the discharge of a single receptor.

It might finally be noted that a study of Ib afferent responses provides the experimenter with an unique opportunity not only to study the physiology of the receptors themselves but also, like the nervous system to which they communicate, to gain information about the behaviour of single motor units.

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